OBSERVATIONS ON THE CHAETOTAXY OF THE LEGS IN THE FREE-LIVING GAMASINA (ACARI : MESOSTIGMATA)

BY

G. OWEN EVANS

Department of Zoology, British Museum (Natural History)

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CONTENTS

SYNOPSIS

Studies on the chaetotaxy of the legs of the free-living Gamasina have shown that segmental chaetotactic patterns provide valuable taxonomic criteria for the classification of the group. The application of leg chaetotaxy to the classification of the Gamasina at species, genus and family levels is discussed. A system of setal nomenclature is introduced for individual leg segments.

INTRODUCTION

During the last ten years, studies on the chaetotaxy of the idiosoma and the gnathosoma of the Mesostigmata have resulted in the introduction of many new taxonomic criteria for the classification of the group. These studies are now extended to the ambulatory appendages which have been largely ignored in both descriptive and classificatory works on the Mesostigmata.

The present contribution is restricted to an account of the leg chaetotaxy in the free-living Gamasina. My studies are as yet incomplete, particularly as regards the ontogenetic development of the chaetotaxy, but they do indicate that leg chaetotaxy can provide taxonomic characters of comparable value to those based on the chaetotaxy of the gnathosoma and idiosoma. It is hoped that this paper will stimulate other acarologists to investigate further this interesting aspect of the morphology of the Mesostigmata.

TERMINOLOGY

For the purpose of setal nomenclature, each segment of the legs is considered to have four setae-bearing surfaces, namely, a dorsal (*d*), a ventral (*v*), an antero-lateral (*al*) and a postero-lateral (*pl*). The anterior and posterior faces of the segment (or leg) refer to the positions adopted when the leg is extended laterally, that is, at right angles to the longitudinal axis of the idiosoma. The setae on the dorsal and ventral surfaces of a segment are divided into an anterior and a posterior series according to their positions relative to the anterior and posterior faces of the segment. The setae are numbered from the distal to the proximal end of the segment. When the distribution of the setae is such that their division into an anterior and posterior series is not possible, they are simply referred to as dorsal (*d*) and ventral (*v*) setae. The unpaired setae which appear during ontogeny on the dorsal and ventral surfaces of tarsi II–III are termed medio-dorsal (*md*) and medio-ventral (*mv*), respectively. The chaetotaxy of tarsus I is not considered in the present study.

It is often necessary to refer to the number of setae on a particular segment of the leg in the course of descriptive work. A reference to the total number of setae is of limited value since it gives no indication of the distribution of the setae on a segment. Considerably more information is given when the numerical data are divided into four sections to coincide with the four setae-bearing faces of the segment. Thus, the data may be expressed as follows:

$$\left(\text{antero-laterals} \;\Big/\; \frac{\text{dorsals}}{\text{ventrals}} \;\Big/\; \text{postero-laterals}\right).$$

Each segmental formula is accompanied by a specific reference to the segment and to the postembryonic developmental stage to which the data apply. For example, Femur I, L $(2 \;/\; \frac{4}{2} \;/\; 2)$ implies that the femoral segment of leg I in the larva bears two antero-laterals, four dorsals, two ventrals and two postero-laterals. The abbreviations L, P, D, A (♂ or ♀) are used, respectively, for larva, protonymph, deutonymph and adult (male and female). This type of segmental formula has been found to be adequate for representing the chaetotactic data of the trochanter and femur but not of the genu and tibia. In many instances, it has been found that the total number of setae on the dorsal and ventral surfaces of the genu and tibia may be the same in widely separated groups of species although the actual chaetotactic patterns of these segments may be quite different owing to differences in the numbers of setae in the anterior and posterior series of the dorsal and/or ventral surfaces of the segments. These differences in chaetotactic patterns may be shown numerically by extending the above chaetotactic formula to include the number of setae in the anterior and posterior series of the dorsal and ventral surfaces, thus,

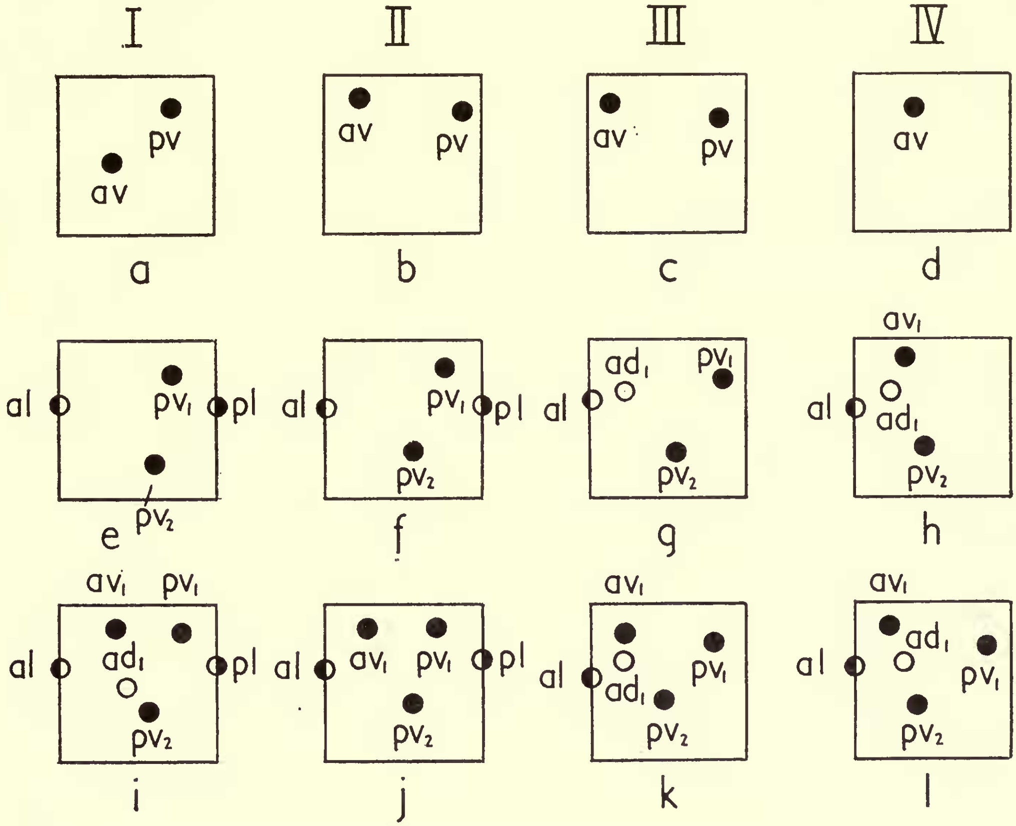
$$\left(\text{antero-laterals} \;\Big/\; \frac{\text{antero-dorsals}}{\text{antero-ventrals}}, \frac{\text{postero-dorsals}}{\text{postero-ventrals}} \;\Big/\; \text{postero-laterals}\right).$$

This formula is used for the chaetotaxy of the genua and tibiae throughout this paper.

In the diagrammatic representation of segmental chaetotaxy, the open cicrcles (○) refer to dorsal setae, the black dots (•) to ventral setae and the half-open circles (◐) to lateral setae.

THE ONTOGENETIC DEVELOPMENT OF THE CHAETOTAXY OF THE LEGS IN *PERGAMASUS* (PARASITIDAE)

The following account of the development of the leg chaetotaxy in the larval and protonymphal stages of *Pergamasus* applies to the majority of the free-living Gamasina I have examined. The adult chaetotaxy which is determined at the deutonymphal stage is considerably more variable.



FIGS. 1*a–l*. Diagrammatic representations of the chaetotaxy of the coxae and trochanters of legs I–IV in *Pergamasus* (Parasitidae). *a–d*, chaetotaxy of the coxae of legs I–IV. *e–h*, chaetotaxy of the trochanters of legs I–IV in the larva and protonymph. *i–l*, chaetotaxy of trochanters I–IV in the deutonymph and adult.

ad, antero-dorsal seta ; *al*, antero-lateral seta ; *av*, antero-ventral seta ; *pd*, postero-dorsal seta ; *pl*, postero-lateral seta ; *pv*, postero-ventral seta; I–IV, legs I–IV.

Coxae I–IV (Text-figs. 1*a–d*)

The chaetotaxy of coxae I–III is determined at the larval stage ; each segment bearing two ventral setae (*av* and *pv*). There is a remarkable constancy in the relative positions of the setae. Coxa IV bears a single ventral seta in the protonymph and in the succeeding developmental stages. This seta is possibly homologous to seta *av* of coxae II and III but has moved to a median position on the segment. The migration of a seta to a median position on the dorsal, ventral and lateral surfaces of a segment when the corresponding member of the pair is missing, is a common feature of segmental chaetotaxy.

Trochanters I–IV (Text-figs. 1*e–l*)

Trochanter I has four setae in the larva and protonymph, comprising two laterals (*al* and *pl*) and two ventrals (pv_1 and pv_2). Two setae are added to the segment in the deutonymph, one dorsal (*d*) and one ventral (*av*). This chaetotaxy is retained by the adult. The chaetotaxy of trochanter II in the larva and protonymph is similar to that of trochanter I at those stages but in the deutonymph only one seta (*av*) is added to the segment. Four setae occur on trochanter III in the larva and on trochanters III and IV in the protonymph, and five setae on each of these segments in the deutonymph and adult. The distribution of these setae is more variable than the setae of trochanters I and II. This is probably due to the asymmetrical development of the trochanters (and femora) of legs III and IV as the result of the posterior direction of legs III and IV.

Femora I–IV (Text-figs. 2*a–i*)

Femora I and II have a completely different chaetotaxy from femora III and IV as regards the number and the distribution of the setae.

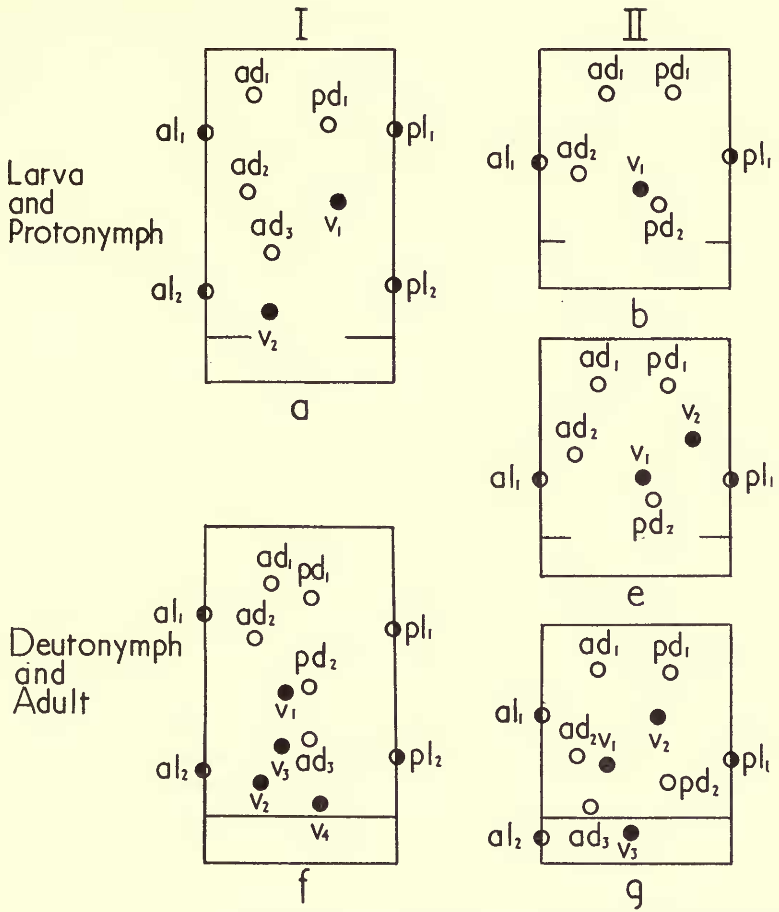
Femur I in the larval and protonymphal stages bears ten setae—four dorsals (ad_1, ad_2, ad_3 and pd_1), four laterals (al_1, al_2, pl_1 and pl_2) and two ventrals (v_1 and v_2). The deutonymphal complement of thirteen setae is formed by the addition of one dorsal (pd_2) and two ventrals (v_3 and v_4). This number is retained by the adult. There are no setae situated proximal of the lyriform fissure. Setae pd_2 and ad_3 assume a median position on the dorsal surface of the segment.

Femur II in the larva (Text-fig. 2*b*) has seven setae (ad_1, ad_2, pd_1, pd_2, v_1, al_1 and pl_1). In the protonymph (Text-fig. 2*e*) a single ventral seta (v_2) is added to the segment whilst in the deutonymph (Text-fig. 2*g*) three setae appear, one lateral (al_2), one dorsal (ad_3) and one ventral (v_3). Setae al_2 and v_3 are situated proximal to the lyriform fissure. The chaetotaxy of the female resembles that of the deutonymph but in the male the segment becomes swollen and seta v_1 and often v_2 hypertrophy and form spur-like structures. The main femoral spur develops from seta v_1 and the axillary spur from seta v_2. Seta v_3 in the male moves to a more distal position and never lies proximal to the lyriform fissure.

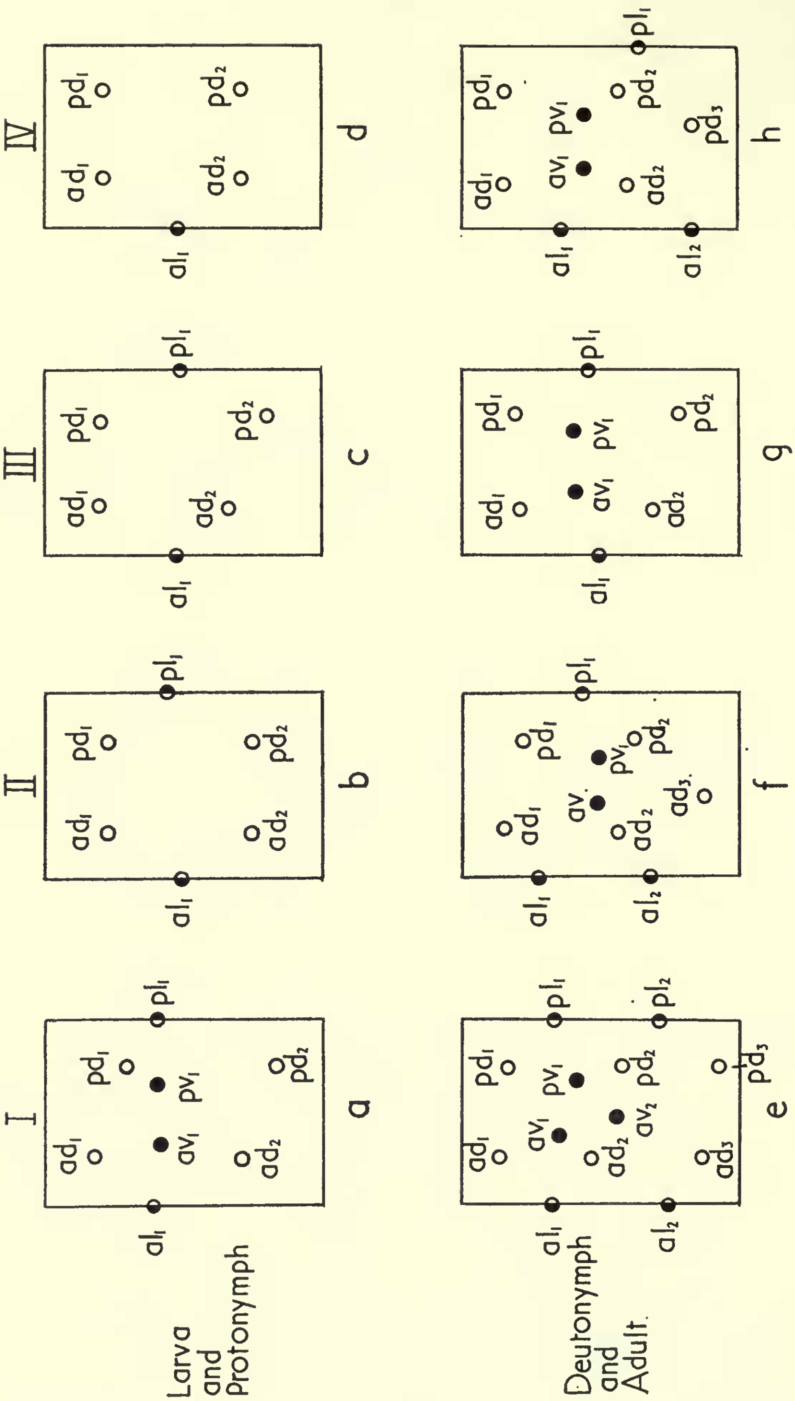
Femur III in the larva and protonymph carries five setae, comprising three dorsals (ad_1, ad_2 and pd_1), one lateral (*al*) and one ventral (*v*). Only one seta (pd_2) is added to the segment in the deutonymph. The chaetotaxy of femur IV in the protonymph resembles that of femur III at that stage except for the absence of the ventral seta (*v*) which appears with pd_2 in the deutonymph. The deutonymphal chaetotaxy of femora III and IV is retained by the adult.

Genua I–IV (3*a–h*)

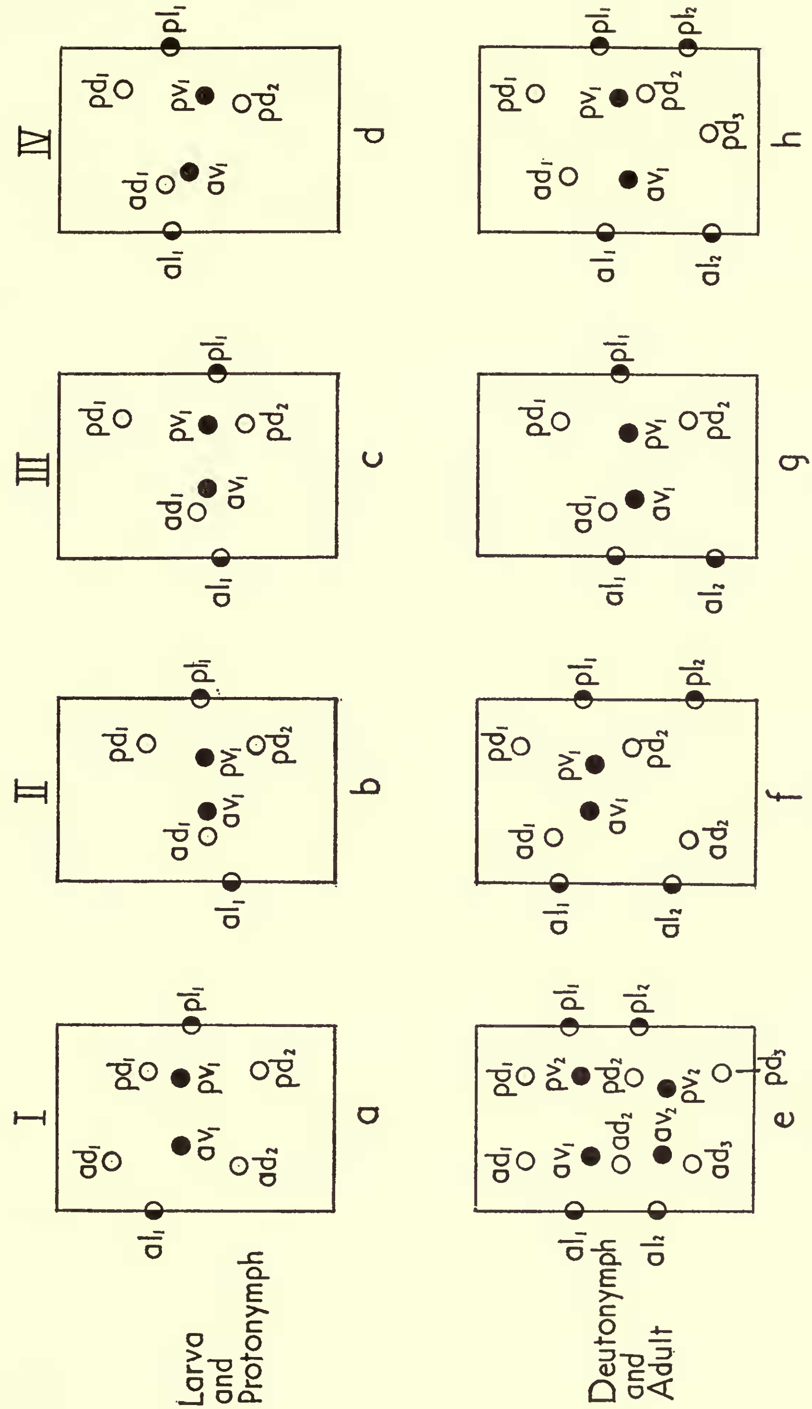
Genu I carries eight setae in the larva and protonymph—four dorsals (ad_1, ad_2, pd_1, pd_2), two laterals (al_1 and pl_1) and two ventrals (av_1 and pv_1). This number is increased to thirteen in the deutonymph by the appearance of one ventral (av_2), two laterals (al_2 and pl_2) and two dorsals (ad_3 and pd_3). Seta av_2 migrates medially so that the three ventral setae form an inverted triangle. Six setae occur on genu II



Figs. 2*a–i*. Diagrammatic representations of the chaetotaxy of the femora of legs I–IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.



FIGS. 3*a–h*. Diagrammatic representations of the chaetotaxy of the genua of legs I–IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.



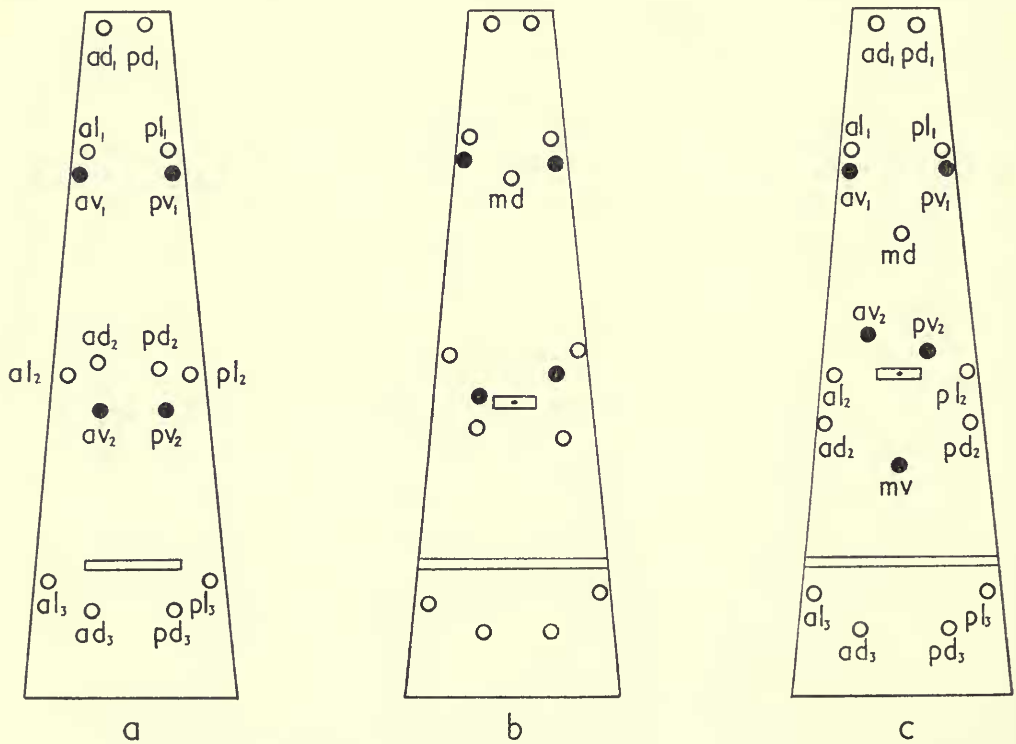
FIGS. 4*a–h*. Diagrammatic representations of the chaetotaxy of the tibiae of legs I–IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.

in the larva and protonymph comprising ad_1, ad_2, pd_1, pd_2, al_1 and pl_1. There are no ventral setae. Five setae appear in the deutonymph, one dorsal (ad_3), two lateral (al_2 and pl_2) and two ventral (av_1 and pv_1). The chaetotaxy of genu III in the larva and protonymph is similar to that of genu II at those stages but only two setae, the ventrals av_1 and pv_1, are added in the deutonymph. Genu IV bears five setae (ad_1, ad_2, pd_1, pd_2 and al_1) in the larva and protonymph. The deutonymph adds five setae (av_1, pv_1, al_2, pl_1 and pd_3).

The deutonymphal chaetotaxy of the genua is retained by the adult. In the males seta av_1 hypertrophies and takes the form of a spur-like structure.

Tibiae I–IV (Text-figs. 4*a–h*)

Tibia I in the larva and protonymph bears eight setae (ad_1, ad_2, pd_1, pd_2, al_1, pl_1, av_1 and pv_1). Six setae are added proximally in the deutonymph. These comprise two dorsals (ad_3 and pd_3), two laterals (al_2 and pl_2) and two ventrals (av_2 and pv_2). The deutonymphal complement of setae is retained by the adult. The tibiae of legs II and III in the larva and protonymph bear seven setae. Their chaetotaxy resembles that of tibia I in these stages except for the absence of ad_2 and the migration of ad_1 to a median position on the segment. Tibia II in the deutonymph shows an



FIGS. 5*a–c*. Diagrammatic representations of the chaetotaxy of tarsi II–IV in the larva (*a*), the protonymph (*b*) and the deutonymph (*c*) of *Pergamasus*.
md, medio-dorsal seta; *mv*, medio-ventral seta. Other abbreviations as in Fig. 1.

increase of three setae—a dorsal (*ad_2*) and two laterals (*al_2* and *pl_2*). Only one seta (*al_2*) is added to tibia III in the deutonymph. The chaetotaxy of tibia IV in the protonymph is similar to that of tibiae II and III at that developmental stage. In comparison with tibia III, however, three setae appear on the segment in the deutonymph (setae *al_2*, *pd_3* and *pl_2*). In the male seta *av_1* may hypertrophy and form a spur-like structure.

Tarsi II–IV (Text-figs. 5*a–e*)

The chaetotaxy of tarsi II and III in the larva consists of sixteen setae—three pairs of dorsals, three pairs of laterals and two pairs of ventrals. In the protonymph an unpaired seta (*md*) is added in the distal half of each of tarsi II–IV and a further unpaired seta (*mv*) appears ventrally in the proximal half in the deutonymph making a total of eighteen setae. This number is retained by the adult.

The chaetotactic formulae for the trochanters, femora, genua and tibiae of legs I–IV in the adults and immature stages of *Pergamasus* are as follows :

Trochanter

L, P, I $(1-\frac{0}{2}-1)$, II $(1-\frac{0}{2}-1)$, III $(1-\frac{1}{2}-0)$, P, IV $(1-\frac{1}{2}-0)$.
D, A, I $(1-\frac{1}{3}-1)$, II $(1-\frac{0}{3}-1)$, III $(1-\frac{1}{3}-0)$, IV $(1-\frac{1}{3}-0)$.

Femur

L, I $(2-\frac{4}{2}-2)$, II $(1-\frac{4}{1}-1)$, III $(1-\frac{3}{1}-0)$.
P, I $(2-\frac{4}{2}-2)$, II $(1-\frac{4}{2}-1)$, III $(1-\frac{3}{1}-0)$, IV $(1-\frac{3}{0}-0)$.
D, A, I $(2-\frac{5}{4}-2)$ II $(2-\frac{5}{3}-1)$, III $(1-\frac{4}{1}-0)$, IV $(1-\frac{4}{1}-0)$.

Genu

L, P, I $(1-\frac{2}{1}, \frac{2}{1}-1)$, II $(1-\frac{2}{0}, \frac{2}{0}-1)$, III $(1-\frac{2}{0}, \frac{2}{0}-1)$, P, IV $(1-\frac{2}{0}, \frac{2}{0}-0)$.
D, A, I $(2-\frac{3}{2}, \frac{3}{1}-2)$, II $(2-\frac{3}{1}, \frac{2}{1}-2)$, III $(1-\frac{2}{1}, \frac{2}{1}-1)$, IV $(2-\frac{2}{1}, \frac{3}{1}-1)$.

Tibia

L, P, I $(1-\frac{2}{1}, \frac{2}{1}-1)$, II $(1-\frac{1}{1}, \frac{2}{1}-1)$, III $(1-\frac{1}{1}, \frac{2}{1}-1)$, P, IV $(1-\frac{1}{1}, \frac{2}{1}-1)$.
D, A, I $(2-\frac{3}{2}, \frac{3}{2}-2)$, II $(2-\frac{2}{1}, \frac{2}{1}-2)$, III $(2-\frac{1}{1}, \frac{2}{1}-1)$, IV $(2-\frac{1}{1}, \frac{3}{1}-2)$.

CHAETOTAXY OF THE LEGS IN THE ADULTS OF THE FREE-LIVING GAMASINA

Coxae I–IV

The chaetotaxy of the coxae is constant in the free-living Gamasina ; the details given for the developmental stages of *Pergamasus* (p. 279) applying throughout the group. The form of the coxal setae varies considerably. In *Scarabaspis* (Eviphididae), for example, both setae of coxa I and seta *pv* of coxa II take the form of sclerotized oval protuberances.

Trochanters I–IV

Trochanter I in the majority of the species I have examined bears six setae—two laterals (*al* and *pl*), three ventrals (*av*, pv_1, pv_2) and one dorsal (*d*). The Microsejidae, however, retain the larval complement of four setae in the adult, and in the families Macrochelidae and Phytoseiidae (with few exceptions) and the genus *Thinoseius* (Eviphididae) there are only five setae on this segment ; the dorsal seta (*d*) being absent. The relative positions of the setae are remarkably constant.

The chaetotaxy of trochanter II is essentially the same in all the species investigated and comprises five setae (*al*, av_1, pv_1, pv_2 and *pl*). With the exception of *Microgynium* (Microsejidae), the occurrence of five setae on trochanters III and IV is also constant although the distribution of the setae on the segments is variable. In *Microgynium*, trochanter III has only four setae, thus retaining the larval pattern.

The setae on the trochanters appear to be concentrated towards the external face of the segment when the legs are in the normal position for ambulation, that is, on the posterior surfaces of trochanters I and II and the anterior surfaces of trochanters III and IV.

Femur I

Four types of chaetotaxy of femur I have been observed :

X-type $(2-\frac{4}{3}-1)$.

The chaetotaxy comprises setae al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, v_1, v_2 and v_3 (Text-fig. 6*a*). The three ventral setae form an inverted triangle. I have observed this chaetotactic pattern only in the Microsejidae (*Microsejus* and *Microgynium*).

XI-type $(2-\frac{5}{2}-2)$.

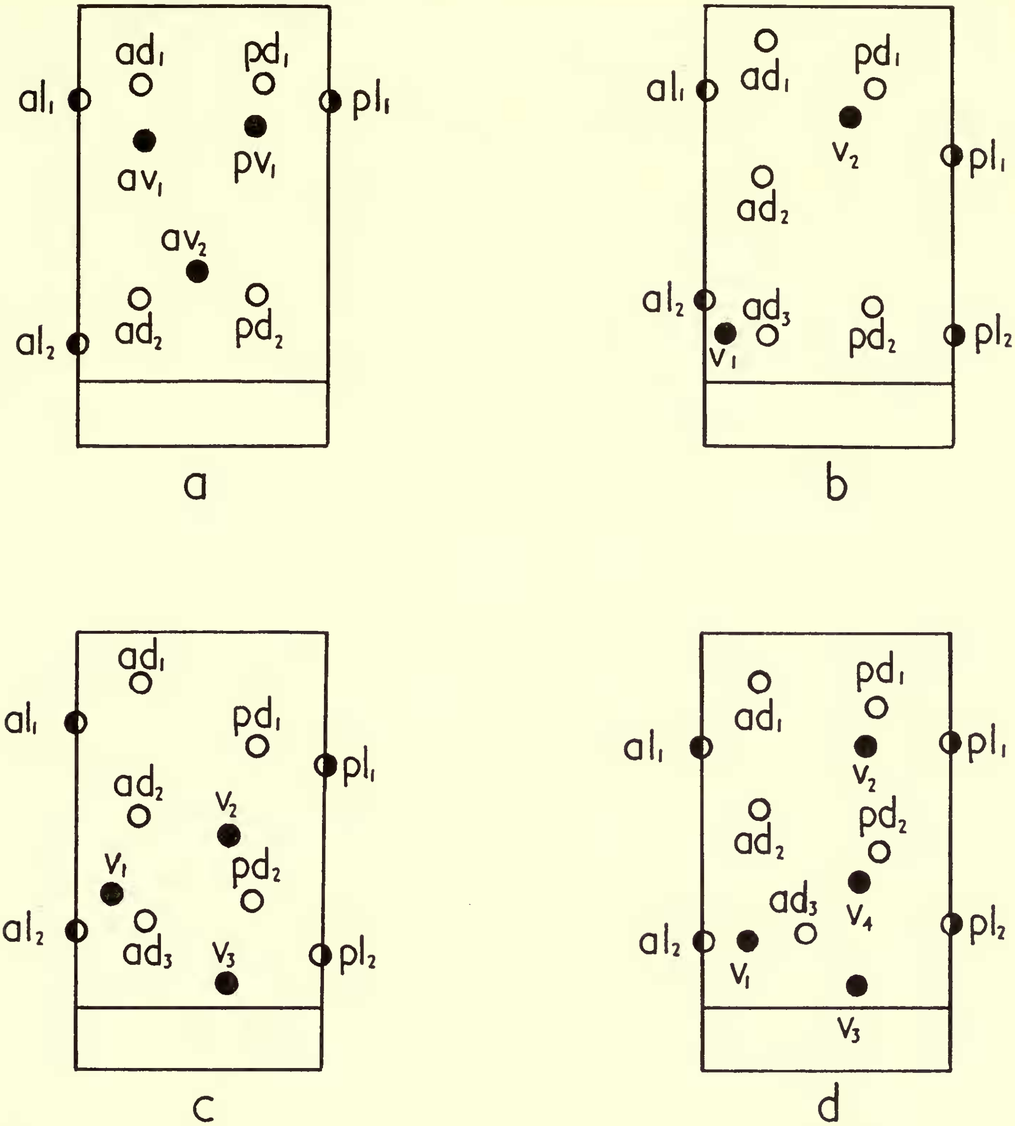
The following setae are present : al_1, al_2, ad_1, ad_2, ad_3, pd_1, pd_2, pl_1, pl_2, v_1 and v_2 (Text-fig. 6*b*). This type occurs in the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae) and *Thinoseius* (Eviphididae).

XII-type $(2-\frac{5}{3}-2)$.

Seta v_3 is added to those occurring in the XI-type making three ventral setae (Text-fig. 6*c*). This chaetotaxy occurs in the families Phytoseiidae and Ameroseiidae, and in the genera *Asca* and *Halolaelaps* (Rhodacaridae) and the genera *Lasioseius*, *Proctolaelaps*, *Melichares*, *Leioseius*, *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae).

XIII-type $(2-\frac{5}{4}-2)$.

This type is characterized by having four ventral setae (Text-fig. 6*d*). It is the most widely distributed chaetotactic pattern in the suborder and has been observed in the families Parasitidae, Veigaiaidae, Arctacaridae, Laelaptidae, Zerconidae, Epicriidae, Macrochelidae and Pachylaelaptidae, and in the genera *Eviphis*, *Alliphis*, *Pelethiphis* and *Scarabaspis* (Eviphididae), and *Rhodacarus*, *Rhodacarellus*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).



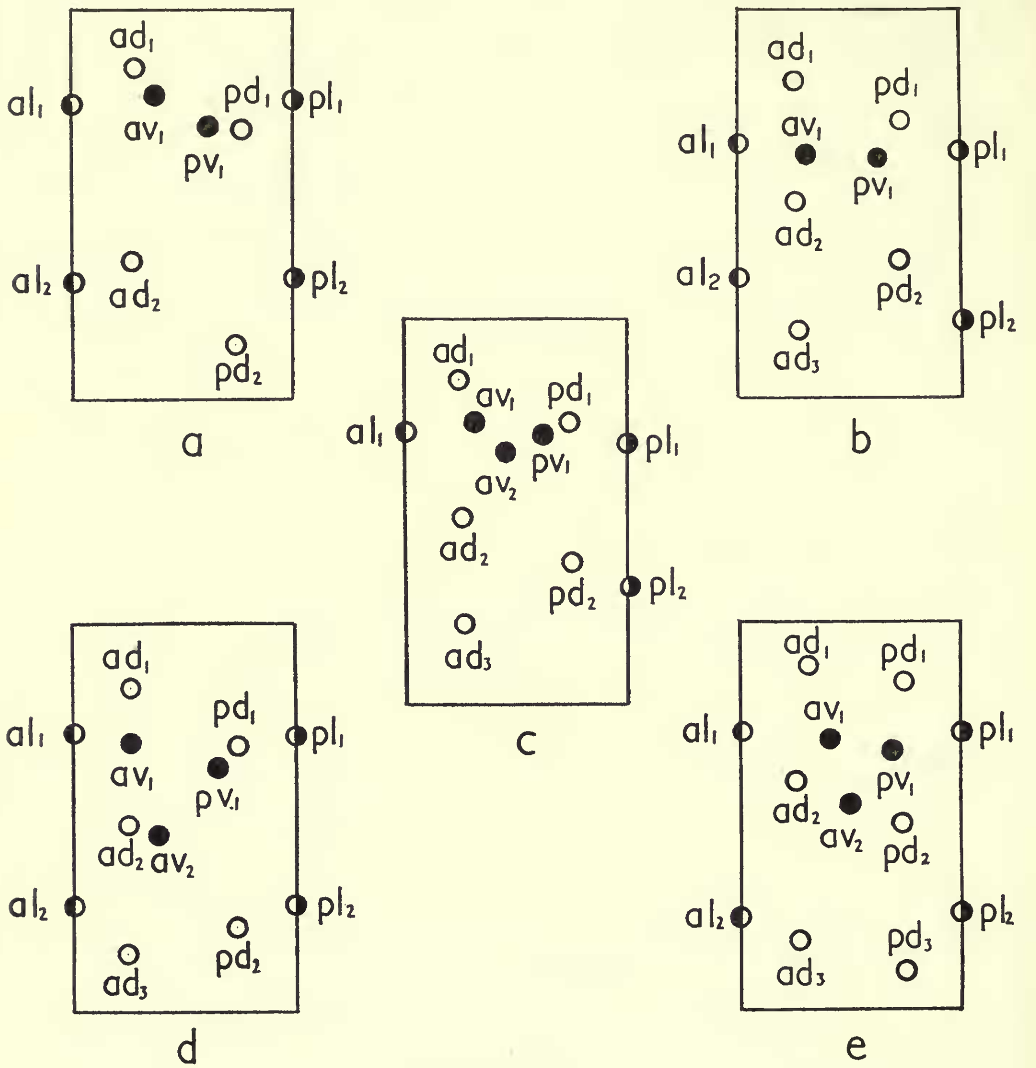
FIGS. 6*a–d*. Diagrammatic representation of the chaetotaxy of femur I in the free-living Gamasina, *a*, **X-type** (Microsejidae). *b*, **XI-type** (Aceosejidae). *c*, **XII-type** (Ameroseiidae). *d*, **XIII-type** (Eviphididae).
Abbreviations as in Fig. 1.

Genu I

I have observed five types of chaetotactic patterns of genu I; the number of setae ranging from ten to thirteen.

X-type $(2-\frac{2}{1}, \frac{2}{1}-2)$.

The following setae are present: ad_1, ad_2, pd_1, pd_2, av_1, pv_1, al_1, al_2, pl_1, pl_2 (Text-fig. 7*a*). This type is characteristic of members of the families Phytoseiidae and Microsejidae.



FIGS. 7*a–e*. Diagrammatic representations of the chaetotaxy of genu I in the free-living Gamasina. *a*, **X-type** (Phytoseiidae). *b*, **XIb-type** (Macrochelidae). *c*, **XIa-type** (Eviphididae). *d*, **XII-type** (Aceosejidae). *e*, **XIII-type** (Parasitidae).
Abbreviations as in Fig. 1.

XIa-type $(1-\frac{3}{2}, \frac{2}{1}-2)$.

This chaetotactic pattern differs from all others on genu I in having a single antero-lateral (al_1) seta. The setal complement is al_1, ad_1, ad_2, ad_3, pd_1, pd_2, pl_1, pl_2, av_1, av_2 and pv_1 (Text-fig. 7*c*). I have only observed this pattern in the Eviphididae.

XIb-type ($2-\frac{3}{1}, \frac{2}{1}-2$).

This differs from the X-type in having an additional dorsal seta, ad_3 (Text-fig. 7*b*). It is characteristic of the Macrochelidae.

XII-type ($2-\frac{3}{2}, \frac{2}{1}-2$).

This chaetotactic pattern is similar to XIb except for the presence of an additional ventral seta (av_2). The three ventral setae form an inverted triangle owing to the migration of seta av_2 to a median position on the segment (Text-fig. 7*d*). It is found in the Ameroseiidae and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Asca*, *Digamasellus* and *Halolaelaps* (Rhodacaridae) and *Pachyseius* (Pachylaelaptidae).

XIII-type ($2-\frac{3}{2}, \frac{3}{1}-2$).

The XIII-type is characterized by having six dorsal (ad_1–ad_3 and pd_1–pd_3), in addition to two antero-laterals, two postero-laterals and three ventrals (Text-fig. 7*e*). I have observed this genual pattern in the families Parasitidae, Veigaiaidae, Arctacaridae, Laelaptidae, Zerconidae and Epicriidae, and in the genera *Lasioseius Proctolaelaps*, *Melichares*, *Leioseius*, *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), *Pachylaelaps* and *Olopachys* (Pachylaelaptidae) and *Rhodacarus*, *Rhodacarellus*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).

Tibia I

The X–XIII-types of chaetotaxy observed on genu I also occur on tibia I as well as a XIV-type characterized by having four ventral setae.

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

This type (Text-fig. 8*a*) is found in the families Phytoseiidae and Microsejidae.

XI-type ($1-\frac{3}{2}, \frac{2}{1}-2$).

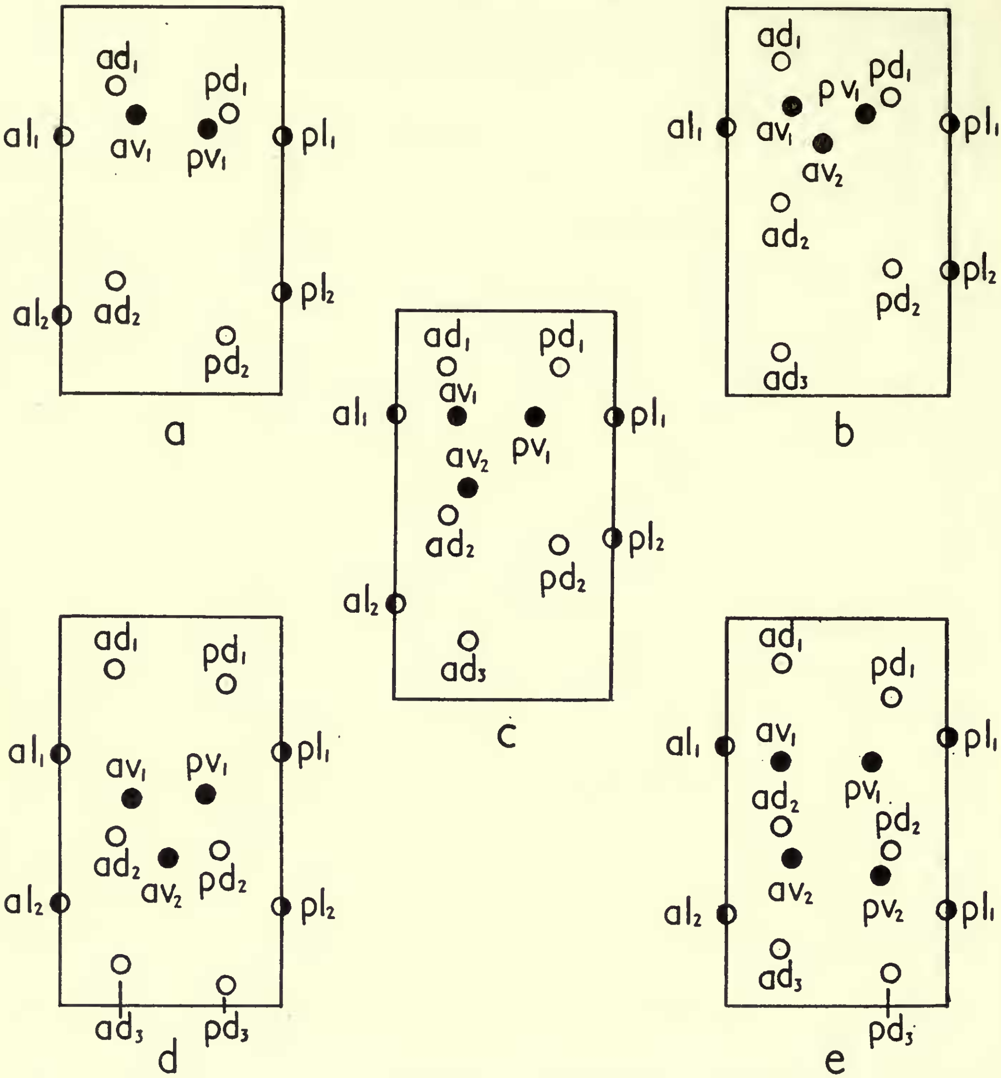
Only the XIa-type of chaetotaxy of genu I occurs on the tibia and as in the case of the genu it appears to be restricted to members of the family Eviphididae (Text-fig. 8*b*).

XII-type ($2-\frac{3}{2}, \frac{2}{1}-2$).

This type (Text-fig. 8*c*) occurs in the families Macrochelidae, Pachylaelaptidae and Ameroseiidae, and in the genera *Arctoseius*, *Iphidozercon*, *Zerconopsis* and *Plesiosejus* (Aceosejidae), and *Digamasellus* and *Halolaelaps* (Rhodacaridae).

XIII-type ($2-\frac{3}{2}, \frac{3}{1}-2$).

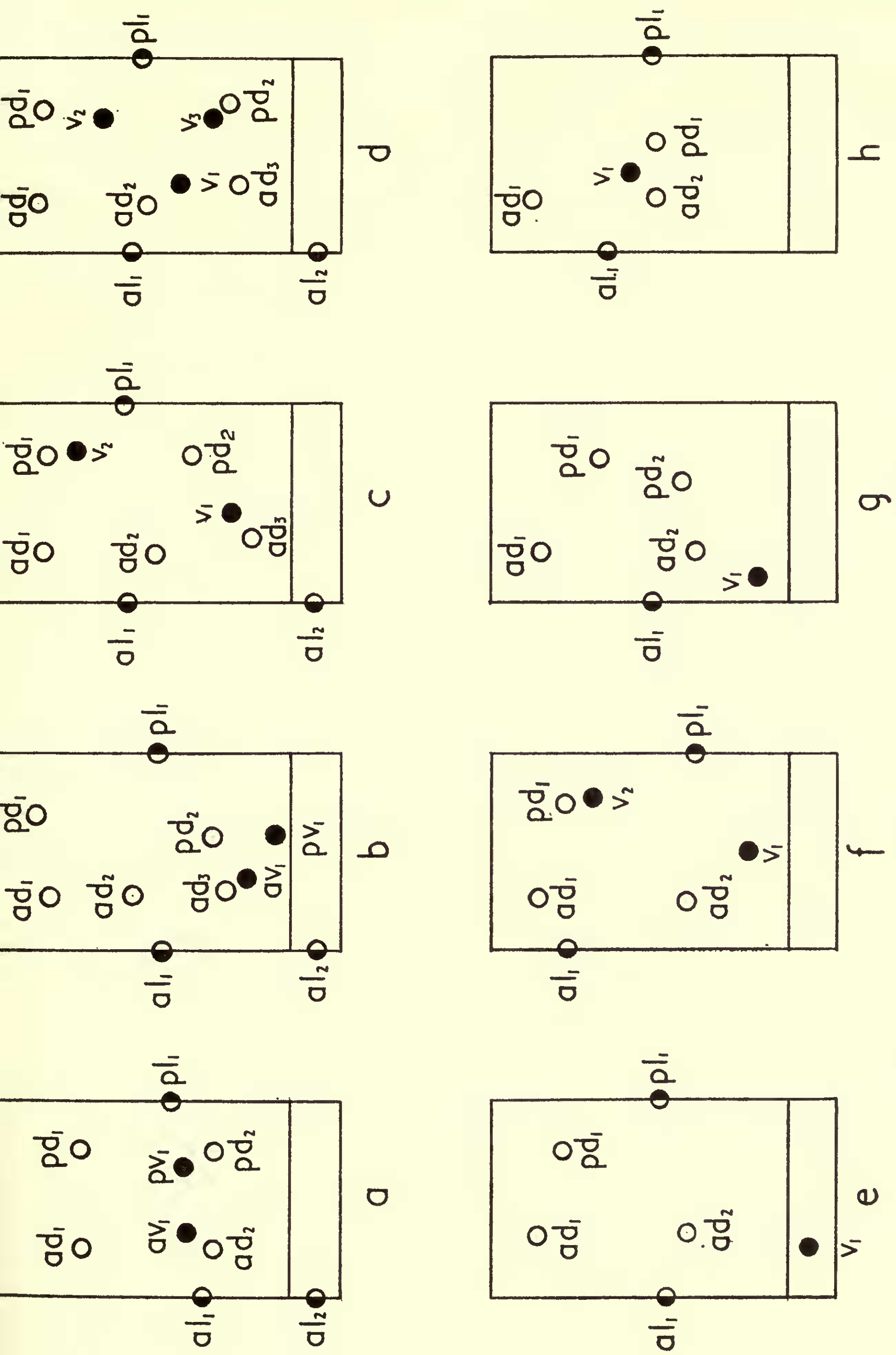
I have observed this chaetotactic pattern (Text-fig. 8*d*) in the free-living Laelaptidae and in the genera *Lasioseius*, *Proctolaelaps*, *Melichares*, *Leioseius*, *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), and *Asca* (Rhodacaridae).



FIGS. 8*a–e*. Diagrammatic representations of the chaetotaxy of tibia I in the free-living Gamasina. *a*, **X-type** (Phytoseiidae). *b*, **XI-type** (Eviphididae). *c*, **XII-type** (Aceosejidae). *d*, **XIII-type** (Aceosejidae). *e*, **XIV-type** (Parasitidae).
Abbreviations as in Fig. 1.

XIV-type $(2-\frac{3}{2}, \frac{3}{2}-2)$.

The four ventral setae arranged in the form of a rectangle readily distinguishes this pattern from the others found on tibia I (Text-fig. 8*e*). It occurs in the families Parasitidae, Veigaiaidae, Arctacaridae, Zerconidae, Epicriidae and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).



FIGS. 9*a*–*h*. Diagrammatic representations of the chaetotaxy of femora II–IV in the free-living Gamasina. *a*, Femur II, **IX-type** (Microsejidae). *b*, Femur II, **Xb-type** (Phytoseiidae). *c*, Femur II, **Xb-type** (*Thinoseius*; Eviphididae). *d*, Femur II, **XI-type** (Laelaptidae). *e*, Femur III, **VI-type** (Parasitidae). *f*, Femur III, **VII-type** (*Thinoseius*: Eviphididae). *g*, Femur IV, **VI-type** (Parasitidae). *h*, Femur IV, **VI-type** (Plesiosejus: Aceosejidae).

Abbreviations as in Fig. 1.

Femur II

The following four types of chaetotactic pattern have been observed on this segment:

IX-type $(2-\frac{4}{2}-1)$.

This type has the following chaetotaxy; al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, av_1 and pv_1 (Text-fig. 9*a*). It occurs in the Microsejidae.

Xa-type $(2-\frac{4}{3}-1)$.

The chaetotaxy comprises ad_1, ad_2, pd_1, pd_2, al_1, al_2, pl_1, v_1, v_2 and v_3. This type has been found in the family Ameroseiidae.

Xb-type $(2-\frac{5}{2}-1)$.

The chaetotaxy differs from the Xa-type in the presence of five dorsal setae (ad_3 additional) but only two ventral setae. It is characteristic of the Phytoseiidae, the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), and also occurs in the genus *Thinoseius* (Eviphididae). In the latter, the ventral setae are widely separated so that one occurs in the proximal and the other in the distal half of the segment (Text-fig. 9*c*). In the Phytoseiidae, however, both ventral setae are usually situated in the proximal half of the segment (Text-fig. 9*b*).

XI-type $(2-\frac{5}{3}-1)$.

This type has five dorsal setae and three ventrals in addition to the two antero-laterals and one postero-lateral (Text-fig. 9*d*). It is the most widely distributed chaetotactic pattern of femur II in the Gamasina and has been observed in the families Parasitidae, Veigaiaidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Laelaptidae, Macrochelidae, Pachylaelaptidae, Aceosejidae (with the exception of *Sejus*, *Platyseius* and *Plesiosejus*) and Eviphididae (excluding *Thinoseius*).

Seta al_2 is always situated proximal to the lyriform fissure in all four types of chaetotaxy.

Genu II

Genu II carries seven, nine, ten or eleven setae.

VII-type $(2-\frac{2}{0}, \frac{2}{0}-1)$.

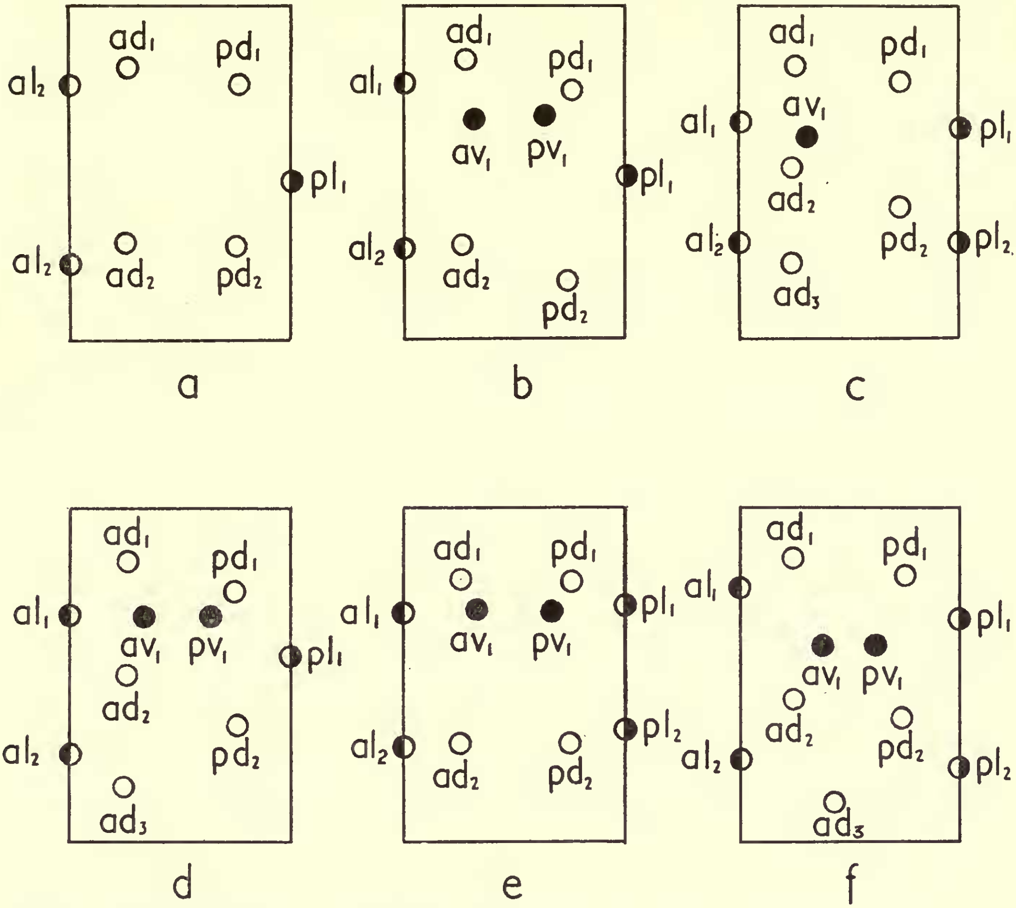
In this type there are no ventral setae (Text-fig. 10*a*); the chaetotaxy comprising setae al_1, al_2, ad_1, ad_2, pd_1, pd_2 and pl_1. It occurs in the majority of the Phytoseiidae.

IX-type $(2-\frac{2}{1}, \frac{2}{1}-1)$.

I have, to date, only observed this pattern in *Amblyseius graminis* Chant (Phytoseiidae). The chaetotaxy shows an addition of two ventral setae (av_1 and pv_1) to the VII-type (Text-fig. 10*b*).

Xa-type $(2-\frac{2}{1}, \frac{2}{1}-2)$.

This differs from the IX-type in having two postero-lateral setae (Text-fig. 10*e*). This pattern is characteristic of the Microsejidae.



FIGS. 10*a–f*. Diagrammatic representations of the chaetotaxy of genu II in the free-living Gamasina. *a*, **VII-type** (Phytoseiidae). *b*, **IX-type** (*Amblyseius graminis* Chant : Phytoseiidae). *c*, **Xc-type** (*Sejus* : Aceosejidae). *d*, **Xb-type** (Aceosejidae). *e*, **Xa-type** (Microsejidae). *f*, **XI-type** (Parasitidae).
Abbreviations as in Fig. 1.

Xb-type $(2-\frac{3}{1}, \frac{2}{1}-1)$.

This type (Text-fig. 10*d*) which occurs in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae) is characterized by having two antero-laterals (al_1 and al_2), five dorsals (ad_{1-3} and pd_{1-2}), two ventrals (av_1 and pv_1) and one postero-lateral (pl_1).

Xc-type $(2-\frac{3}{1}, \frac{2}{0}-2)$.

The Xc-type has two postero-laterals but only one ventral seta (Text-fig. 10*c*). It occurs in the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae).

Xd-type $(1-\frac{3}{1}, \frac{2}{1}-2)$.

This pattern differs from all others on genu II in having only one antero-lateral seta. I have observed this chaetotaxy in the genus *Thinoseius* (Eviphididae) only.

XI-type $(2-\frac{3}{1}, \frac{2}{1}-2)$.

The XI-type (Text-fig. 10*f*) is by far the most widely distributed chaetotactic pattern of this segment and occurs in the families Parasitidae, Veigaiaidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Macrochelidae, Pachylaelaptidae, Laelaptidae, Ameroseiidae and Eviphididae (excluding *Thinoseius*) and in the genera *Lasioseius, Leioseius, Melichares* and *Proctolaelaps* (Aceosejidae).

Tibia II

In the species I have examined, tibia II bears seven, nine or ten setae.

VII-type $(1-\frac{2}{1}, \frac{1}{1}-1)$.

This type is characteristic of the Phytoseiidae and comprises setae al_1, ad_1, ad_2, pd_1, pl_1, av_1 and pv_1 (Text-fig. 11*a*).

IXa-type $(1-\frac{2}{1}, \frac{2}{1}-2)$.

This type, observed only in *Thinoseius* (Eviphididae), has one antero-lateral seta (al_1).

IXb-type $(2-\frac{2}{1}, \frac{2}{1}-1)$.

The chaetotaxy comprises al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, av_1 and pv_2 (Text-fig. 11*b*). This type occurs in the genera *Arctoseius, Iphidozercon* and *Zerconopsis* (Aceosejidae).

IXc-type $(2-\frac{2}{1}, \frac{1}{1}-2)$.

The chaetotaxy comprises setae al_1, al_2, ad_1, ad_2, pd_1, pl_1, pl_2, av_1, pv_1 (Text-fig. 11*c*). I have observed this type in the genera *Platyseius* and *Plesiosejus* (Aceosejidae).

IXd-type $(2-\frac{1}{1}, \frac{2}{1}-2)$.

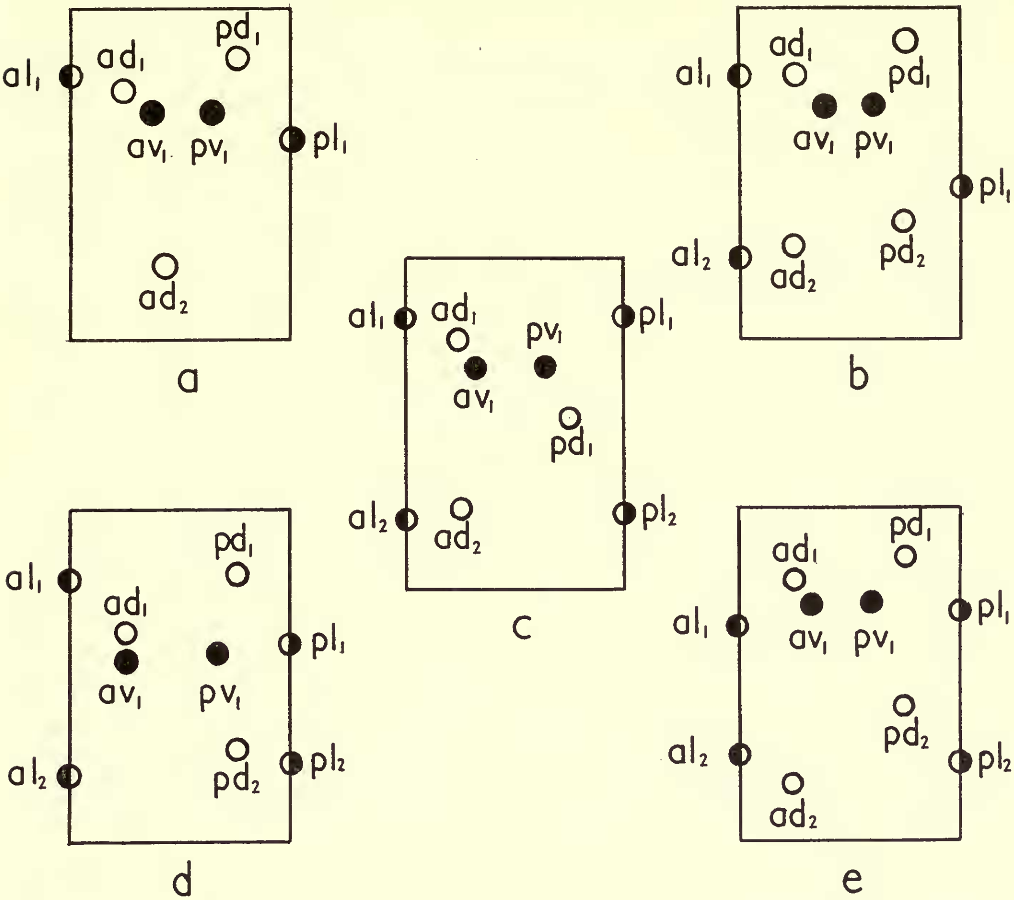
This differs from the IXc-type in the setation of the dorsal surface of the segment ; the three setae being ad_1, pd_1 and pd_2 (Text-fig. 11*d*). It occurs only in the Microsejidae.

X-type $(2-\frac{2}{1}, \frac{2}{1}-2)$.

The following setae are present : al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, pl_2, av_1 *and* pv_1 (Text-fig. 11*e*). This chaetotactic pattern is present in the families Parasitidae, Veigaiaidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Laelaptidae, Ameroseiidae, Macrochelidae, Pachylaelaptidae, Eviphididae (excluding *Thinoseius*) and in the genera *Lasioseius, Leioseius, Melichares, Proctolaelaps* and *Sejus* (Aceosejidae).

Tarsi II–IV

The chaetotaxy of tarsi II–IV is extremely constant throughout the free-living Gamasina ; the details given for *Pergamasus* (p. 278) being applicable throughout. There is some variation in the relative position of the setae due, in some instances, to the elongation of the segment and in the form of setae ad_1 and pd_1.



FIGS. 11*a–e*. Diagrammatic representations of the chaetotaxy of tibia II in the free-living Gamasina. *a*, **VII-type** (Phytoseiidae). *b*, **IXb-type** (*Zerconopsis*: Aceosejidae). *c*, **IXc-type** (*Platyseius*: Aceosejidae). *d*, **IXd-type** (Microsejidae). *e*, **X-type** (Laelaptidae).
Abbreviations as in Fig. 1.

Femur III

The number of setae on femur III is markedly constant. With the exception of *Thinoseius*, all the species I have examined have six setae (Text-fig. 9*e*). Owing to the difference in shape of this segment in certain species, the distribution of the setae is subject to some variation. In *Thinoseius*, seven setae are present; the additional seta apparently being developed ventrally (Text-fig. 9*f*).

Genu III

This segment bears six to ten setae.

VI-type ($1-\frac{2}{0}, \frac{2}{0}-1$).

The following setae are present : al_1, ad_1, ad_2, pd_1, pd_2 and pl_1 (Text-fig. 12*a*). There are no ventral setae. I have seen this type only in the genus *Phytoseius* (Phytoseiidae).

VII-type ($1-\frac{2}{1}, \frac{2}{0}-1$).

The chaetotaxy comprises setae al_1, ad_1, ad_2, pd_1, pd_2, pl_1 and av_1 (Text-fig. 12*b*). It occurs in members of the family Macrochelidae and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Pachylaelaps* and *Olopachys* (Pachylaelaptidae), *Thinoseius* (Eviphididae) and *Iphiseius* and *Typhlodromus* (Phytoseiidae).

VIIIa-type ($1-\frac{2}{1}, \frac{2}{1}-1$).

The chaetotaxy differs from the VII-type in the addition of pv_1 (Text-fig. 12*c*). This chaetotactic pattern occurs in the Eviphididae (excluding *Thinoseius*).

VIIIb-type ($2-\frac{2}{1}, \frac{2}{0}-1$).

This chaetotactic pattern has been found in the genera *Asca* and *Saprolaelaps* (Rhodacaridae), *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), *Pachyseius* (Pachylaelaptidae) and *Epicriopsis* (Ameroseiidae). The eight setae comprise al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1 *and* av_1 (Text-fig. 12*d*).

IXa-type ($2-\frac{2}{1}, \frac{2}{1}-1$).

Setae al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, av_1 and pv_1 are present in this type (Text-fig. 12*e*). This pattern occurs in the families Parasitidae, Veigaiaidae, and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Hydrogamasus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae), *Lasioseius*, *Leioseius*, *Melichares* and *Proctolaelaps* (Aceosejidae), *Hypoaspis*, *Coleolaelaps* and *Ololaelaps* (Laelaptidae) and *Neocypholaelaps* (Ameroseiidae).

IXb-type ($2-\frac{2}{1}, \frac{2}{0}-2$).

I have observed this type only in the Microsejidae (Text-fig. 12*f*).

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

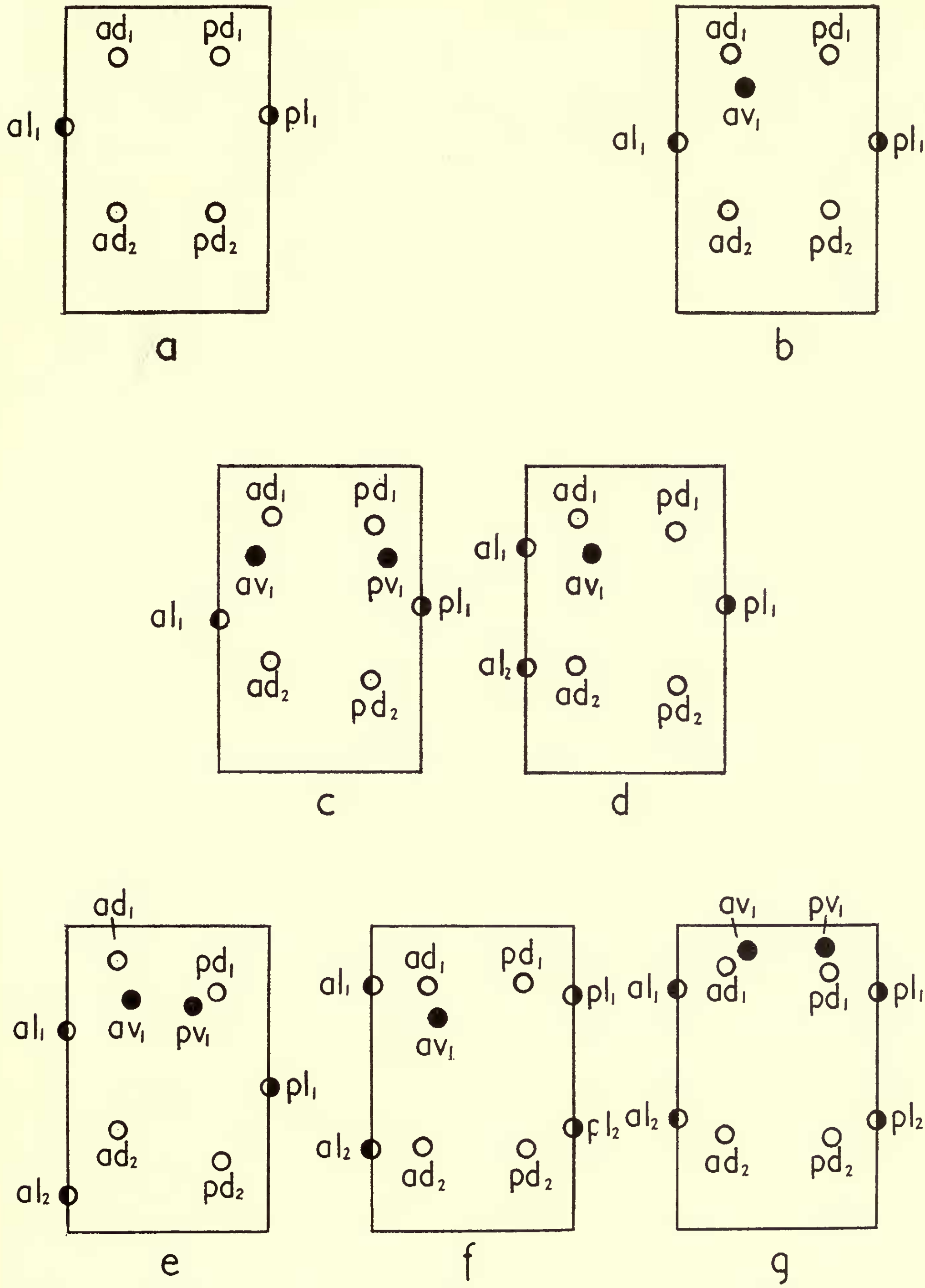
The ten setae comprise al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, pl_2, av_1 and pv_1 (Text-fig. 12*g*). It occurs in the families Arctacaridae, Zerconidae and Epicriidae, and in the genera *Ameroseius* and *Kleemannia* (Ameroseiidae).

Tibia III

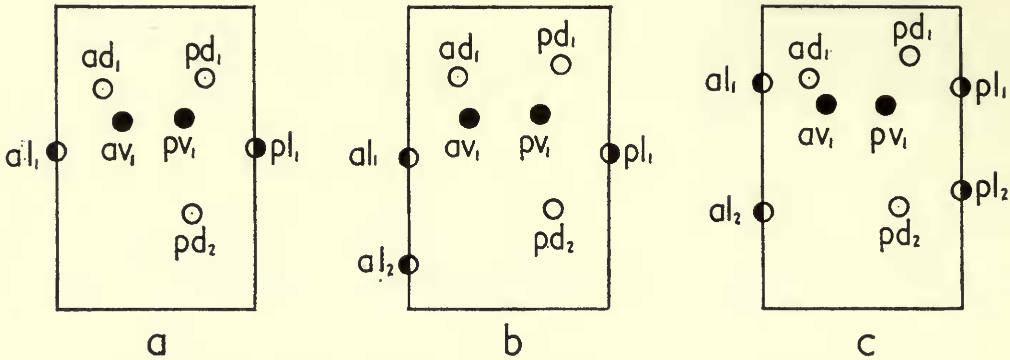
The following three types of chaetotactic pattern have been observed on this segment :

VII-type ($1-\frac{1}{1}, \frac{2}{1}-1$).

This type occurs in the families Phytoseiidae, Eviphididae, Macrochelidae and Pachylaelaptidae, and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae). The chaetotaxy comprises al_1, ad_1, pd_1, pd_2, pl_1, av_1 and pv_1 (Text-fig. 13*a*).



FIGS. 12*a–g*. Diagrammatic representations of the chaetotaxy of genu III in the free-living Gamasina. *a*, **VI-type** (*Phytoseius*: Phytoseiidae). *b*, **VII-type** (Macrochelidae). *c*, **VIIIa-type** (Eviphididae). *d*, **VIIIb-type** (*Asca*: Rhodacaridae). *e*, **IXa-type** (Parasitidae). *f*, **IXb-type** (Microsejidae). *g*, **X-type** (Zerconidae). Abbreviations as in Fig. 1.



FIGS. 13*a–c*. Diagrammatic representations of the chaetotaxy of tibia III in the free-living Gamasina. *a*, **VII-type** (Phytoseiidae). *b*, **VIII-type** (Parasitidae). *c*, **IX-type** (Microsejidae).
Abbreviations as in Fig. 1.

VIII-type $(2-\frac{1}{1}, \frac{2}{1}-1)$.

There is an addition of one antero-lateral seta to the VII-type ; the seta being al_2 (Text-fig. 13*b*). This pattern is present in the families Parasitidae, Veigaiaidae, Rhodacaridae, Laelaptidae, Ameroseiidae (excluding *Kleemannia*) and in the genera *Lasioseius*, *Leioseius*, *Melichares* and *Proctolaelaps* (Aceosejidae).

IX-type $(2-\frac{1}{1}, \frac{2}{1}-2)$.

Seta pl_2 is additional to the VIII–type (see Text-fig. 13*c*). It occurs in the families Arctacaridae, Zerconidae, Epicriidae and Microsejidae and in the genus Kleemannia (*Ameroseiidae*).

Femur IV

The presence of six setae on this segment is extremely constant in the free-living Gamasina ; the only exception being members of the Microsejidae. In the majority of the species I have examined the chaetotaxy comprises al_1, ad_1, ad_2, pd_1, pl and v_1 (Text-fig. 9*h*) but there are variants of this pattern as, for example, in the aceosejid *Plesiosejus* (Text-fig. 9*g*) which has four dorsals but no postero-lateral setae. The microsejids have seven setae on this segment (al_1, ad_1, ad_2, pd_1, pd_2, av_1 and pv_1).

Genu IV

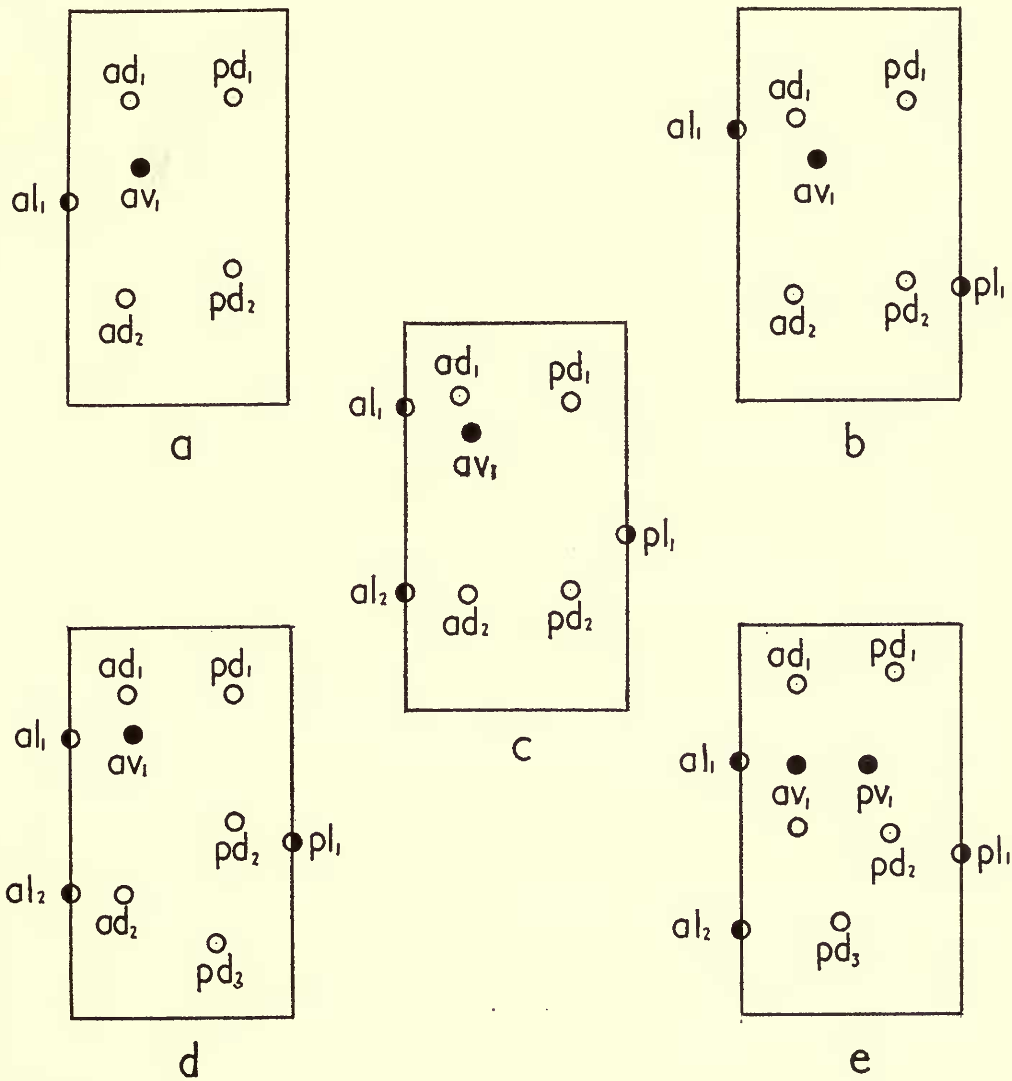
Five types of chaetotaxy of genu IV have been observed.

VI-type $(1-\frac{2}{1}, \frac{2}{0}-0)$.

The following setae are present : al_1, ad_1, ad_2, pd_1, pd_2 and av_1 (Text-fig. 14*a*). This pattern is found in certain species of the genus *Macrocheles* s.lat. (Macrochelidae) and has been used as a taxonomic character by Evans & Hyatt (1962).

VII-type $(1—\frac{2}{1}, \frac{2}{0}—1)$.

This shows an addition of seta *pl* to the VI-type (Text-fig. 14*b*). It is found in the families Pachylaelaptidae, Eviphididae and Phytoseiidae, in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Digamasellus* (Rhodacaridae) and certain species of the Macrochelidae.



FIGS. 14*a–e*. Diagrammatic representations of the chaetotaxy of genu IV in the free-living Gamasina. *a*, **VI-type** (*Macrocheles*: Macrochelidae). *b*, **VII-type** (Eviphididae). *c*, **VIII-type** (Microsejidae). *d*, **IX-type** (*Lasioseius*: Aceosejidae). *e*, **X-type** (Parasitidae).

Abbreviations as in Fig. 1.

VIII-type $(2-\frac{2}{1}, \frac{2}{0}-1)$.

Setae al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1 and av_1 are present (Text-fig. 14*c*). This type occurs in the family Microsejidae.

IX-type $(2-\frac{2}{1}, \frac{3}{0}-1)$.

Seta pd_3 is added to the VIII-type (Text-fig. 14*d*). It is found in the families Laelaptidae, Ameroseiidae and in the genera *Lasioseius*, *Leioseius*, *Melichares*, *Proctolaelaps*, *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), and in *Asca* and *Halolaelaps* (Rhodacaridae).

X-type $(2-\frac{2}{1}, \frac{3}{1}-1)$.

This type (Text-fig. 14*e*) has two ventral setae (pv_1 being additional to the ventral chaetotaxy found in the other types). It occurs in the families Parasitidae, Veigaiaidae, Arctacaridae, Zerconidae, Epicriidae and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Hydrogamasus* and *Gamasiphis* (Rhodacaridae).

Tibia IV

Six types of chaetotaxy of tibia IV have been observed ; the number of setae on the segment ranging from six to ten.

VI-type $(1-\frac{1}{1}, \frac{2}{0}-1)$.

This type comprising setae al_1, ad_1, pd_1, pd_2, pl_1 and av_1 occurs in members of the family Phytoseiidae (Text-fig. 15*a*).

VII-type $(1-\frac{1}{1}, \frac{2}{1}-1)$.

The chaetotaxy of this type differs from VI in the addition of one postero-ventral seta (Text-fig. 15*b*). It is found in the families Macrochelidae, Pachylaelaptidae and Eviphididae, and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae) and *Digamasellus* (Rhodacaridae).

VIII-type $(2-\frac{1}{1}, \frac{2}{1}-1)$.

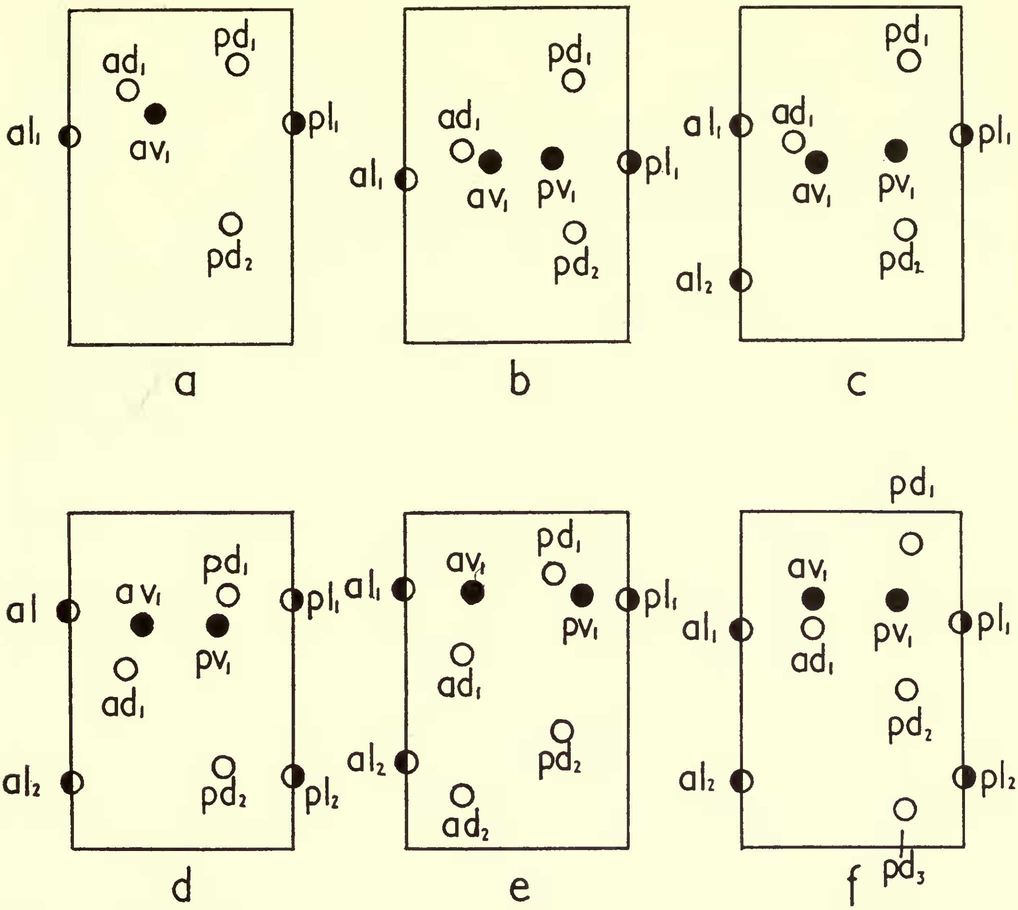
I have found this type in the genus *Halolaelaps* (Rhodacaridae) and the chaetotactic pattern differs from the VII-type in the addition of seta al_2 (Text-fig. 15*c*).

IXa-type $(2-\frac{2}{1}, \frac{2}{1}-1)$.

The chaetotaxy comprises al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, av_1 and pv_1 (Text-fig. 15*e*). The pattern occurs in the family Ameroseiidae.

IXb-type $(2-\frac{1}{1}, \frac{2}{1}-2)$.

In contrast to type IXa, the segment bears only one antero-dorsal seta (ad_1) but two postero-lateral setae (pl_1 and pl_2). This type of chaetotaxy occurs in the families Zerconidae and Microsejidae (Text-fig. 15*d*).



FIGS. 15*a–f*. Diagrammatic representations of the chaetotaxy of tibia IV in the free-living Gamasina. *a*, **VI-type** (Phytoseiidae). *b*, **VII-type** (Eviphididae). *c*, **VIII-type** (Halolaelaps : Rhodacaridae). *d*, **IXb-type** (Microsejidae). *e*, **IXa-type** (Ameroseiidae). *f*, **X-type** (Parasitidae).
Abbreviations as in Fig. 1.

X-type $(2-\frac{1}{1}, \frac{3}{1}-2)$.

This type shows an addition of postero-dorsal seta (pd_3) to the setal complement of IXb (Text-fig. 15*f*). It is found in the families Parasitidae, Veigaiaidae, Arctacaridae, Epicriidae and Laelaptidae and Aceosejidae (excluding genera under VII-type), and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Hydrogamasus* and *Gamasiphis*.

DISCUSSION

The wide variety of leg segmental chaetotactic patterns displayed by the free-living Gamasina will undoubtedly provide useful morphological criteria for their classification. Taxonomic characters based on chaetotactic patterns are readily definable quantitatively and are thus suitable for mathematical analysis. The value of chaetotactic patterns as indicators of phylogenetic relationships is difficult to assess although in free-living forms their stability at species, genus and family levels is surprisingly high. However, the nature of the ontogenetic development of the chaetotaxy, particularly the importance of localized neoteny in determining specific segmental patterns in specialized parasitic forms, allows for the widespread occurrence of convergence in chaetotactic patterns. The results of the present study suggest that the overall chaetotaxy of the legs, especially of legs I and II, may be of significance in the classification of the suborder at familial and suprafamilial levels whereas differences in the chaetotaxy of individual segments may be of more value at species and genus level.

Segmental chaetotaxy of the legs appears to be subject to little or no intraspecific variation. In the free-living Gamasina, differences in chaetotactic patterns between species of the same genus are usually restricted to a single segment as, for example, the presence of six or seven setae on genu IV in *Macrocheles* (Evans & Hyatt, 1962). Specialized parasitic forms exhibit considerably more interspecific variation. According to Till (1962), species of the genus *Androlaelaps* show differences in the chaetotaxy of tibia I, tibia III, genu III and genu IV. This variability is even more marked in the endoparasitic forms where differences in overall leg chaetotaxy may be of importance only at species level. Differences in the chaetotaxy of one or two leg segments are also evident at generic level and are particularly useful in providing " key characters" for the differentiation of genera belonging to the same family. For example, the chaetotactic patterns of genu III in the Ameroseiidae, of genua III and IV in the Phytoseiidae and genu III in the Pachylaelaptidae.

An analysis of the leg chaetotaxy in confamilial genera indicates a greater stability in the chaetotaxy of legs I and II than of legs III and IV. With few exceptions, the familial concepts based on leg chaetotaxy support the present classification of the free-living Gamasina based on other morphological criteria. The notable exception is the family Rhodacaridae. The genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Gamasiphis*, *Hydrogamasus* and *Sessiluncus* form a natural assemblage which can be accommodated in the family Rhodacaridae, whereas the genera *Digamasellus*, *Asca* and *Halolaelaps* do not appear to be confamilial with the *Rhodacarus*-group. Their affinities appear to be with certain genera of the Aceosejidae but whether they should be placed in that family or in a distinct family (Digamasellidae) can only be decided by a comprehensive study of the complex. Certainly the emphasis placed on the nature of the dorsal sclerotization of the idiosoma in the classification is not justified in the light of the conclusions reached on the basis of chaetotactic studies.

The criterion of leg chaetotaxy also gives interesting results when applied to the classification of the Aceosejidae. At present this family is divided into two subfamilies (Evans, 1957), namely, the Aceosejinae and Platyseiinae. On the bases of segmental patterns, however, three groups of genera may be recognized of which two groups are more closely related to each other than to the third. The three groups are: (*a*) *Lasioseius*, *Leioseius*, *Proctolaelaps*, *Melichares* and *Zercoseius* (Aceosejinae); (*b*) *Sejus*, *Platyseius* and *Plesiosejus* (Platyseiinae) and (*c*) *Arctoseius*, *Iphidozercon* and *Zerconopsis*. In group (*c*) the genera *Arctoseius* and *Iphidozercon* are at present placed in the Aceosejinae and *Zerconopsis* in the Platyseiinae. This revised grouping of the genera appears to be more satisfactory since members of group (*c*) which may be referred to as the Arctoseiinae, differ from the other two groups in the nature of the chaetotaxy of the opisthonotal region of the dorsal shield in the female. The Arctoseiinae also show affinities with the *Digamasellus*-group mentioned above.

The chaetotaxy of legs I and II also provide good " key characters " for the separation of certain families which have been difficult to distinguish on such characters as idiosomal sclerotization and chaetotaxy. Two such cases immediately come to mind, namely, the separation of the Aceosejidae and Phytoseiidae, and of the Eviphididae and Laelaptidae. Reference to the chaetotactic patterns of the genua and the tibiae of legs I will now remove much of the uncertainty associated with the recognition of members of these families in existing key works.

The results of isolated observations on the leg chaetotaxy of the Uropodina and Antennophorina (or Fedrizzina) suggest that segmental chaetotaxy is also of importance at all levels of their classification. In the Uropodina, for example, there is a marked and constant difference between the segmental chaetotaxy of the Lower Uropodina (Trachytid-type) and the more specialized Higher Uropodina (Uropodid-type) ; the latter exhibiting considerably more localized neoteny in leg chaetotaxy to the extent of certain segments retaining the larval chaetotaxy in the adult stages. A comprehensive study of the leg chaetotaxy in the Uropodina is now being undertaken by Mr. Brian Ainscough.

The Mesostigmata, in common with the Anactinochaeta as a whole, display little variety in setal types. Unlike the Actinochaeta which have a variety of setal types that can be distinguished on the basis of their optical and chemical properties (Grandjean, 1935), the setae of the leg segments of the Mesostigmata referred to in the present work appear to be of one type. They are solid and lack " actinochitin ". The sensory field distally on tarsus I, however, has a variable number of hollow setae which bear a superficial resemblance to the solenidia of certain Actinochaeta.

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